2003. The Journal of Arachnology 31:78–89

HABITAT AFFINITIES OF SPIDERS LIVING NEAR A FRESHWATER POND

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ABSTRACT. Habitat ranges of ground-dwelling spiders were studied by pitfall trapping in and around a freshwater pond during the spring and summer of 1998 in central Alberta, Canada. Sixty species from 14 families were collected, and catches of several species suggested distinct habitat affinities along transects between the pond and adjacent terrestrial habitats. Variation in the catches of *Pirata piraticus* (Clerck 1757), *Pardosa moesta* Banks 1892, *Pardosa fuscula* (Thorell 1875), and immature *Pirata* species were partially explained by soil moisture at trap locations extending from the shore. We devised a "floating" pitfall trap that captured several species, including mature and immature *Dolomedes triton* (Walckenaer 1837), *Pirata piraticus*, and other immature Lycosidae, directly on the water surface. A DCA ordination revealed distinct spider assemblages were associated with three habitat types: 1) the water surface; 2) the moist habitats closely associated with the water's edge; and 3) the drier, terrestrial grassland habitats located >2 m from the shore. A new, more inclusive definition of semi-aquatic spiders was developed, based on knowledge about both male and female activity near the shore, and affinities towards soil moisture. Thus, *Pirata piraticus*, *Dolomedes triton*, and *Pardosa fuscula* were defined as semi-aquatic spiders.

Keywords: Habitat gradient, soil moisture, semi-aquatic, floating pitfall trap

Many spiders are associated with freshwater ecosystems. For example, the diversity and general ecology of spiders inhabiting peatlands in Canada, Denmark and Germany have been examined (Nørgaard 1951; Dondale & Redner 1994; Schikora 1994), as has the spider fauna of rice fields (e.g., Heiss & Meisch 1985; Oraze & Grigarick 1989). Much work has also focused on the biology and habitat affinities of nursery web spiders (Pisauridae), especially those in the genus *Dolomedes* Latreille 1804 (e.g., Bleckmann & Lotz 1987; Zimmermann & Spence 1989, 1998; Jordan et al. 1994). Few detailed studies of spider assemblages living near freshwater habitats such as small ponds exist, however, so little is known about the diversity, abundance, and habitat selection of semi-aquatic spiders outside of bogs and rice fields.

Aquatic organisms derive respiratory oxygen entirely from the surrounding water environment (Miall 1895). The term "semiaquatic" has been used to refer to organisms that spend part of their lives in or on water, but which generally obtain oxygen from the air (Ward 1992). Under this definition, *Dolomedes triton* (Walckenaer 1837), found at the margins of ponds, is accurately described as semi-aquatic. This spider is capable of moving rapidly over the surface film (Suter & Gruenwald 2000), and does so in response to vibrations of potential insect prey (Shultz 1987). Also, insects such as whirligig beetles (Coleoptera, Gyrinidae) and water striders (Hemiptera, Gerridae), which also forage on the surfaces of freshwater ponds, are considered semi-aquatic (Spence 1986; Merritt & Cummins 1996). However, many species not usually considered to be aquatic or semi-aquatic live and forage in the upper littoral zone of a freshwater body, perhaps because of a moisture preference or requirement.

Spiders in various families occur around bodies of water. Some spiders, in particular wolf spiders (Lycosidae), are commonly collected in ombrotrophic bogs (Nørgaard 1951; Itamies & Jarva-Karenlampi 1989), so one might expect to find them in or near a freshwater pond. Spiders in the family Linyphiidae have long been known to have affinities with moisture (Huhta 1965), and many build small webs on damp ground near the surface of wa-

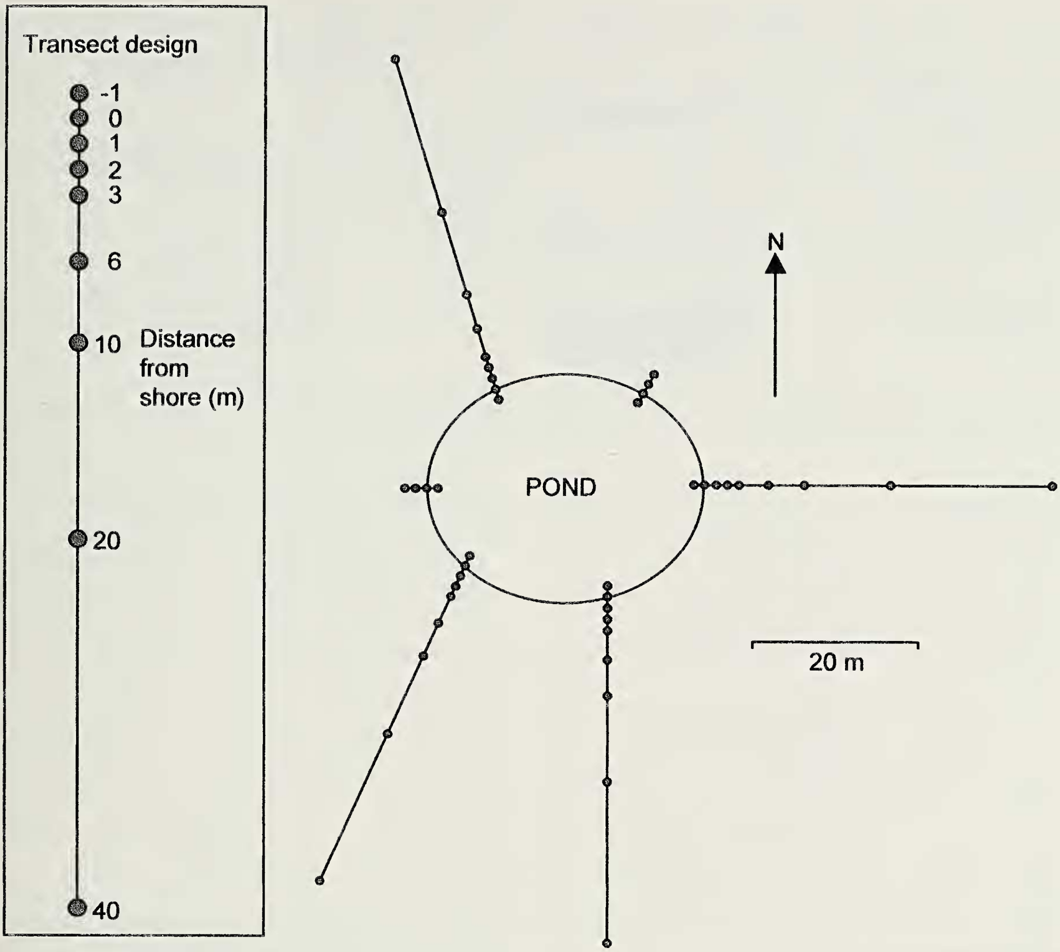

Figure 1.—Sampling design, depicting series of pitfall traps (circles, 6 floating, 38 terrestrial) along transects extending from a freshwater pond.

ter (Kaston 1981). Pisaurids and hahniids are also commonly observed near freshwater (Carico 1973; Opell & Beatty 1976; Suter 1999).

In this study we used pitfall traps to collect gound-dwelling spiders along a habitat gradient starting with the pond surface and extending into the adjacent terrestrial system. We sought to determine: 1) which ground-dwelling species have affinities to the aquatic habitat; 2) the relationship between species abundance and soil moisture; and 3) which species have the potential to forage on the water surface.

METHODS

Study sites and sampling design.—This research was conducted at the George Lake Field Site (53°57′N, 114°06′W), located approximately 85 km NW of Edmonton, Alberta, Canada. Habitats in and around "Meadow Pond" were chosen for study. This permanent freshwater pond, measuring about 22 by 29 m, was constructed in 1970 in a small meadow cleared from continuous upland *Populus* forest the previous year. The pond was surrounded immediately by mixed grasses and short shrubs, and a forest dominated by *Populus* trees was located 30–40 m from the pond's edge [see Niemelä et al. (1992) for detailed description].

Pitfall traps were placed in six transects around the pond (Fig. 1). Four transects consisted of nine traps, the first placed in the pond 1 m from shore ("floating" trap, see description below), and the rest embedded in the ground and extending to a distance of 40 m from the pond as illustrated in Fig. 1. Two

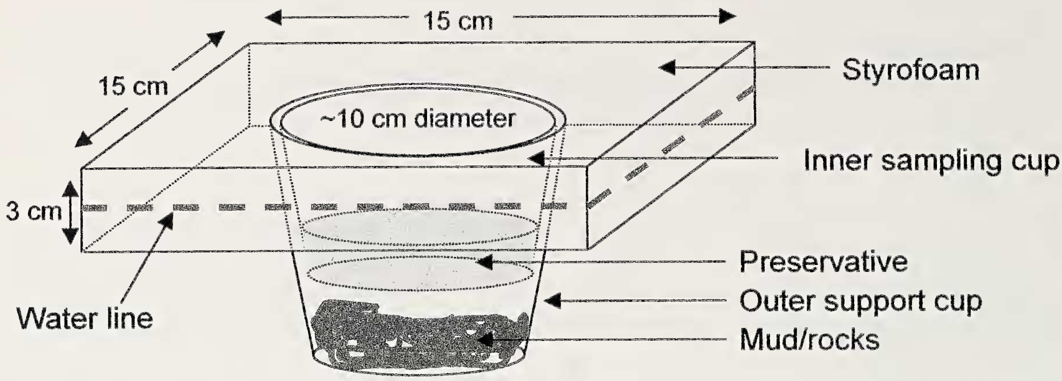

Figure 2.—Design of floating pitfall trap. Styrofoam platform was secured to desired location by an anchoring pole, and covered by a 15 by 15 cm plywood roof (not shown).

shorter transects contained only four traps, the first a floating trap and the others at 0, 1 and 2 m from shore (Fig. 1). Short transects were used specifically to amplify data about spiders living near the shore. Traps were open from 21 May–06 September 1998 and emptied every 10–15 days.

Each terrestrial pitfall trap consisted of a 1 L plastic sleeve container buried so its lip was level with the ground surface. A close-fitting sampling cup containing 2–3 cm of silicate-free ethylene glycol was placed inside each plastic sleeve, and traps were covered with supported plywood roofs (15 by 15 cm) to minimize disturbance and rainwater dilution of the preservative [see Spence & Niemelä (1994) for additional details].

We constructed a novel "floating" pitfall trap to catch skating spiders or those ballooning onto open water. These traps were similar to standard terrestrial pitfall traps, but the plastic containers and sampling cups were held afloat in a one inch thick piece of Styrofoam™ (15 by 15 cm), and weighed down with mud and rocks so that they sat at the water surface (Fig. 2). Each trap was tied to an anchoring pole, and was fitted with a plywood roof measuring 15 by 15 cm.

Soil samples were taken with a circular metal soil corer (15 cm diameter) along each transect at 0, 2, 6 and 20 m from the shore to obtain gravimetric estimates of percent soil moisture along the habitat gradient. Soil samples were taken in early July to coincide with the general peak in spider activity around Meadow Pond. Also, we took the samples five days after a heavy rainfall to ensure that the soil was not over-saturated in certain locations. All samples were weighed, allowed to dry for a week at 40°C and then reweighed.

Spider identifications.—Individual spiders were sorted and identified using various taxonomic keys (e.g., Dondale & Redner 1978, 1982, 1990; Kaston 1981; Platnick & Dondale 1992) and reference collections at the Strickland Entomological Museum (University of Alberta, Edmonton, Alberta, Canada). If necessary, species identifications were verified by D.J. Buckle. Since species identifications are based primarily on genitalia, only sexually mature spiders were identified to species—juveniles were identified to genus whenever possible. Voucher specimens are deposited in the Strickland Entomological Museum.

Data analyses.—Pitfall trap captures depend on movement of individuals and therefore estimate activity and density of species, as well as their susceptibility to trapping (Topping & Sunderland 1992). Since pitfall traps measure this "activity-density," it is difficult to truly detect both absolute abundance and male to female ratios (e.g. Topping &Sunderland 1992; Spence & Niemelä 1994). Even with these limitations, however, pitfall traps are still among the most commonly used sampling technique for collecting spiders, and can offer significant insights into the biology, ecology, life-history and habitat affinities of spiders (e.g., Uetz & Unzicker 1976; Pajunen et al. 1995; Buddle 2000; Buddle et al. 2000). Capture data from the pond transects were analyzed graphically to portray general trends in relative abundance of common species (defined as those comprising >1% of the total catch), separated by gender, as a function of distance from the shore. Since trapping effort varied with distance from shore (i.e., short transects increased sampling effort near shore), data were presented as the number collected per trap.

Linear regression was used to test if soil moisture was related to trap distance from the shore, and to determine whether the catches of common species and numbers of immatures were dependent upon the gradient in relative soil moisture. Data lacking homogeneity of variance were transformed [$x' = \ln(x+1)$] prior to regression analyses.

Data were also interpreted by detrended correspondence analysis (DCA), an ecological ordination technique useful in revealing variations among data and identifying critical factors associated with species distribution patterns (Jongman et al. 1995). Ordination analyses were done using the program PC-ORD (McCune & Mefford 1999); all species were included in the analysis but rare species were downweighted in proportion to their frequency. Rare species were defined as those represented by fewer than F/5 individuals, where F represents the frequency of the most common species collected (McCune & Mefford 1999). Immature specimens were excluded prior to analysis.

RESULTS

Spider species and habitat ranges.—In total, 3145 individuals representing a rich spider assemblage that included 60 species in 14 families were collected by pitfall trapping across the transects (Table 1). Nine common species (i.e., represented by >50 individuals, or >1% of the total collection) composed about 72% of the total catch, and *Pardosa moesta* Banks 1892 alone made up about one third of spiders collected (Table 1). Immature specimens in the genera *Pardosa*, *Pirata*, and *Trochosa* accounted for about 13% of the total collection (Table 1). About 52% of the sexually mature individuals collected were males, and this sex ratio remained similar regardless of of trap location (Table 1).

Several of the more common species were collected at or near the pond shore. *Dolomedes triton* (mature and immature specimens) was trapped most often in floating traps (Table 1), while the relative abundance of *Pirata piraticus* (Clerck 1757) and *Pardosa fuscula* (Thorell 1875) were greatest at the pond shore for both males and females (Figs. 3A, B). Immature *Pirata* were also most frequently collected close to shore (Fig. 3C). Male and female *Neoantistea magna* (Keyserling 1887) were common near the shoreline (Figs. 3D, E), but were also occasionally collected in terrestrial traps located further from the shore (Figs. 3D, E, Table 1). *Pardosa moesta* was more uniformly distributed across the terrestrial traps, although its capture rates were clearly higher between 2 and 10 m from shore (Figs. 3A, B). Patterns with the other common wolf spiders (Lycosidae) were less clear: *Trochosa terricola* Thorell 1856 did not show any affinities towards the pond shore, and immature *Trochosa* were most common about 2–10 m from shore (Figs. 3A, B, C). Collections of immature *Pardosa* were highly variable (Fig. 3C) and thus difficult to assign to any particular region of the habitat gradient. The three most common linyphiids, *Allomengea dentisetis* (Grube 1861), *Bathyphantes pallidus* (Banks 1892) and *Grammonota gigas* (Banks 1896) were generally active in the middle or toward the land-based ends of transects and were rarely collected directly adjacent to the pond shore (Figs. 3D, E). Females of these species were relatively uncommon in our samples (Figs. 3D, E, Table 1).

Although sample sizes were smaller, some of the more rarely collected species (i.e., <50 individuals) also showed affinities towards the shore. For example, immature *Dolomedes*, immature *Neoantistea*, and the linyphiid *Erigone atra* Blackwall 1833 were all most commonly collected <3 m from shore (Table 1). A total of eight taxa were collected in traps floating on the water surface (Table 1). Of these, *Dolomedes triton* (mature and immature), *Pirata piraticus*, and immature *Pirata* were most commonly collected.

Catch rates and soil moisture.—Soil moisture decreased significantly with increasing distance from the shore (linear regression, $Y = 21.29 - 0.58X$, df = 18, $R^2 = 0.25$, $P = 0.028$). Collections of four spider taxa showed significant relationships with relative soil moisture (Fig. 4). Captures of *P. fuscula* and *Pirata piraticus* adults and immature *Pirata* spp. were positively associated with soil moisture (Figs. 4B, C, D). Activity of *P. moesta* showed an opposite trend, increasing as soil moisture decreased (Fig. 4A). The remaining common taxa showed no relationship with our measures of soil moisture.

Table 1.—Summary of spider species collected by floating and terrestrial pitfall traps in or near a freshwater pond. Data provided as MALE/FEMALE, and (IMMATURE) specimens, and totals across all traps. * indicate the most commonly collected taxa.

Family, species	Floating traps	Traps <3 m from shore	Traps 3 to 40 m from shore	Male/ Female Total	TOTAL
Amaurobiidae					
Cybaeopsis euopla (Bishop & Crosby 1935)		0/1	2/10	2/11	13
Immature		(2)	(4)	—	6
Araneidae					
Araniella displicata (Hentz 1847)			0/1	0/1	1
Larinioides cornutus (Clerck 1757)		0/1		0/1	1
Clubionidae					
Clubiona kulczynskii Lessert 1905			1/0	1/0	1
Immature		(1)	(7)	—	8
Gnaphosidae					
Drassyllus niger (Banks 1896)		1/0	1/1	2/1	3
Gnaphosa borea Kulczynski 1908		1/0		1/0	1
Gnaphosa parvula Banks 1896		2/9	4/4	6/13	19
Haplodrassus hiemalis (Emerton 1909)		0/1	4/1	4/2	6
Micaria pulicaria (Sundevall 1832)		1/2	2/2	3/4	7
Zelotes fratis Chamberlin 1920		5/6	15/5	20/11	31
Immature		(10)	(20)	—	30
Hahniidae					
Neoantistea magna (Keyserling 1887)*		78/75	41/8	119/83	202
Neoantistea (immature)		(9)	(3)	—	12
Linyphiidae					
Allomengea dentisetis (Grube 1861)*		11/0	40/7	51/7	58
Aphileta misera (O.P.-Cambridge 1882)			0/1	0/1	1
Bathyphantes pallidus (Banks 1892)*		5/3	31/12	36/15	51
Centromerus sylvaticus (Blackwall 1841)		0/4	0/6	0/10	10
Ceratinella brunnea Emerton 1882			0/1	0/1	1
Ceratinopsis stativa (Simon 1881)		1/0		1/0	1
Diplocentria bidentata (Emerton 1882)		1/0	1/1	2/1	3
Eperigone trilobata (Emerton 1882)			1/0	1/0	1
Erigone atra Blackwall 1833	1/0	8/3	1/2	10/5	15
Gonatium crassipalpum Bryant 1933			1/1	1/1	2
Grammonota gigas (Banks 1896)*		36/11	49/12	85/23	108
Hybauchenidium cymbadentatum (Crosby & Bishop 1935)			0/1	0/1	1
Meioneta sp. A			0/1	0/1	1
Microlinyphia pusilla (Sundevall 1829)		0/4	2/1	2/5	7
Microneta viaria (Blackwall 1841)		0/1	2/1	2/2	4
Neriene radiata (Walckenaer 1841)			0/1	0/1	1
Pityohyphantes costatus (Hentz 1850)			0/1	0/1	1
Pocadicnemis americana Millidge 1975		1/0		1/0	1
Scotinotylus exsectoides Millidge 1981		0/1		0/1	1
Walckenaeria atrotibialis (O.P.-Cambridge 1878)		0/1	2/0	2/1	3
Walckenaeria communis (Emerton 1882)		0/18	0/16	0/34	34
Walckenaeria fusciceps Millidge 1983		1/0		1/0	1
Walckenaeria spiralis (Emerton 1882)		1/0		1/0	1
Zornella cultrigera (L. Koch 1879)			1/0	1/0	1
Immature		(1)	(1)	—	2

Table 1.—Continued.

Family, species	Floating traps	Traps <3 m from shore	Traps 3 to 40 m from shore	Male/ Female Total	TOTAL
Liocranidae					
Agroeca ornata Banks 1892		2/1	1/3	3/4	7
Agroeca pratensis Emerton 1890		3/2	2/9	5/11	16
Scotinella pugnata (Emerton 1890)		1/0		1/0	1
Lycosidae					
Alopecosa aculeata (Clerck 1757)		7/4	6/6	13/10	23
Arctosa emertoni Gertsch 1934		3/4	2/2	5/6	11
Pardosa distincta (Blackwall 1846)			3/0	3/0	3
Pardosa fuscula (Thorell 1875)*		82/65	1/6	83/71	154
Pardosa mackenziana (Keyserling 1877)			0/5	0/5	5
Pardosa moesta Banks 1892*	0/1	147/234	293/421	440/656	1096
Pardosa xerampelina (Keyserling 1877)		6/9	6/8	12/17	29
Pirata insularis Emerton 1885		4/0	1/0	5/0	5
Pirata piraticus (Clerck 1757)*	69/67	242/55	5/5	316/127	443
Trochosa terricola Thorell 1856*		9/43	11/35	20/78	98
Alopecosa (immature)		(1)	(5)	—	6
Arctosa (immatre)		(2)		—	2
Pardosa (immature)*	(4)	(90)	(69)	—	163
Pirata (immature)*	(19)	(72)	(4)	—	95
Trochosa terricola (immature)*	(1)	(58)	(87)	—	146
Mimetidae					
Ero caionis Chamberlin & Ivie 1935			1/0	1/0	1
Pisauridae					
Dolomedes triton (Walckenaer 1837)*	34/21	2/0		36/21	57
Dolomedes (immature)	(20)	(2)		—	22
Salticidae					
Immature		(1)		—	1
Tetragnathidae					
Pachygnatha clercki Sundevall 1830		1/0		1/0	1
Pachygnatha tristriata C.L. Koch 1845			1/1	1/1	2
Pachygnatha sp. A		0/3		0/3	3
Immature	(1)	(4)	(4)	—	9
Theridiidae					
Euryopsi argentea Emerton 1882		0/1		0/1	1
Thomisidae					
Ozyptila sincera canadensis Dondale & Redner 1975		6/0	20/2	26/2	28
Xysticus britcheri Gertsch 1934		1/1	1/1	2/2	4
Xysticus elegans Keyserling 1880		0/1		0/1	1
Xysticus ellipticus Turnbull, Dondale & Redner 1965		4/5	10/0	14/5	19
Xysticus emertoni Keyserling 1880		5/1	16/2	21/3	24
Xysticus ferox (Hentz 1847)		2/0	3/0	5/0	5
Immature		(2)	(12)	—	14
TOTAL	104/89 (45)	680/570 (255)	584/603 (215)	1368/1262	3145

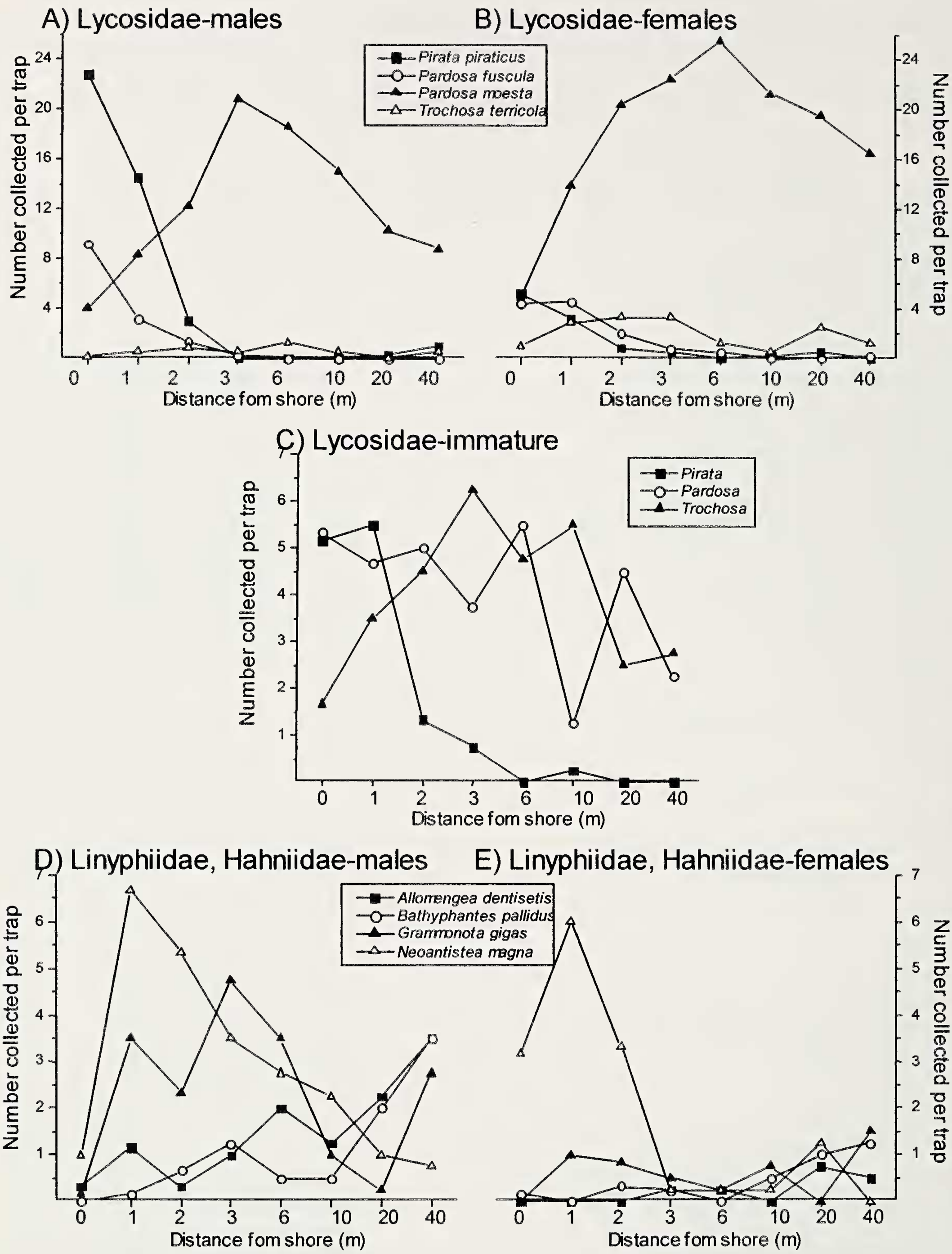

Figure 3.—Number of male, female and immature spiders collected per pitfall trap for common species in the families Lycosidae (A, B, C), Linyphiidae and Hahniidae (D, E) sampled along transects extending from the shore of pond. These taxa account for 84.4% of the total number of individuals collected in all but floating traps.

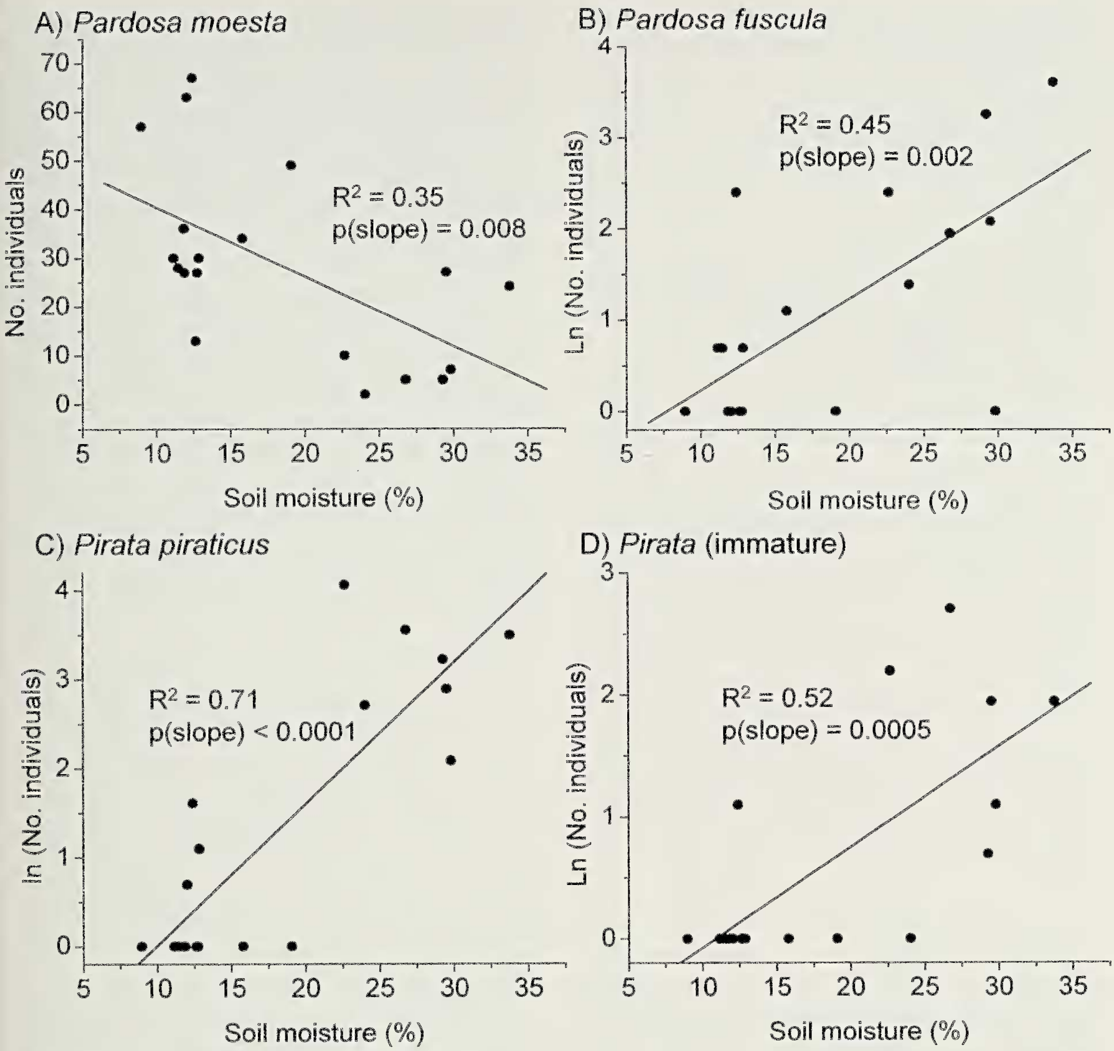

Figure 4.—Linear regression of catches of *Pardosa moesta*, *P. fuscula*, *Pirata piraticus*, and immature *Pirata* against soil moisture (%). All but data for *P. moesta* ln-transformed prior to analyses (note scale on y-axis).

Community patterns.—DCA analysis of data from the 38 terrestrial and 6 floating pitfall traps, and 60 spider species, yielded a high eigenvalue of 0.629 for Axis 1, suggesting that a single environmental variable explains most of the variation in the ordination (Fig. 5). The positions of various traps along the first DCA axis closely reflect their similarity in terms of species composition. Floating traps, which caught the same few species and most *D. triton* (Table 1), grouped together, and shore traps (at shore, 1 m and 2 m from shore) occupied similar positions along Axis 1 (Fig. 5). In particular, species scores for *D. triton*, *Pirata piraticus*, *Pardosa fuscula*, and *Neoantistea magna* were closest to floating traps and the terrestrial pitfall traps close to shore (Fig. 5). Traps at >2 m from the shore had lower scores along Axis 1 and contained more variation along Axis 2. The positions of two traps with high sample scores along Axis 2 are associated with high catches of *A. dentisetis* and *B. pallidus*, as reflected by their species scores (Fig. 5). Species scores for *T. terricola*, *Grammonota gigas*, and *Pardosa moesta* were located more centrally in the ordination space, which reflects their relative ubiquity along sampling transects (Fig. 5).

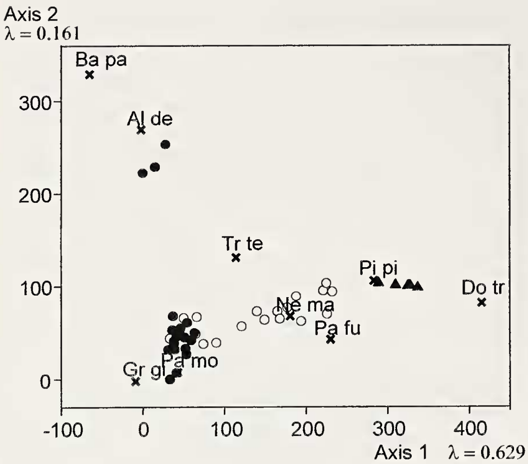

Figure 5.—Sample scores (pitfall traps) and selected species scores from DCA ordination (Axes 1 and 2) derived from 44 samples and 60 spider species. λ indicates eigenvalues for axes 1 and 2. Triangles are floating traps, open circles are terrestrial pitfall traps located at 0, 1, and 2 m from shore, and solid circles are pitfall traps > 2 m from shore. Species scores (**x**) depicted for the 9 most commonly collected species: *Allomengea dentisetis* (Al de), *Bathyphantes pallidus* (Ba pa), *Dolomedes triton* (Do tr), *Grammonota gigas* (Gr gi), *Neoantistea magna* (Ne ma), *Pardosa fuscula* (Pa fu), *Pardosa moesta* (Pa mo), *Pirata piraticus* (Pi pi), and *Trochosa terricola* (Tr te).

DISCUSSION

Habitat ranges.—Our results indicate that a gradient between a pond and an adjacent forest habitat supports a diverse assemblage of spiders, and several common species had strong associations with one part of the gradient. *Pirata piraticus* and *Pardosa fuscula*, for example, were associated with moist littoral areas, *Pardosa moesta* was more common in open, dry grassy regions, and *D. triton* was most often caught on the pond surface.

Habitat ranges of *D. triton*, and *Pirata piraticus* were most strongly associated with the water surface. Since both males and females of these species showed the same distributions in capture rates, it is likely that reproduction is occurring on, at, or near the pond surface. *Dolomedes* species live near permanent bodies of freshwater, such as small ponds and streams (Carico 1973; Shultz 1987; Zimmermann & Spence 1989, 1998; Suter 1999). Our findings for *D. triton* were similar, as our collections of adults of this species were concentrated on the water rather than near the pond (Table 1, Fig. 5). The lycosid genus *Pirata* Sundevall 1833 may be collected near ponds and lakes, or in bogs, swamps, marshes and deep meadows (Wallace & Exline 1978). In our study, *Pirata* species were most common on the pond surface or on land close to the shore. Clearly, *D. triton* and *Pirata piraticus* are active in and strongly associated with the pond's upper littoral zone.

Pardosa moesta alone accounted for 35% of all spiders collected. Males and females were common between 3–10 m from shore although individuals of both sexes were also collected in traps nearer to or farther from the shore. In contrast, *Pardosa fuscula* (males and females) was most common at or near the pond shore (Figs. 3A & B, 5). Others have noted that *P. fuscula* is associated with moist habitats such as peatlands in eastern Canada (Dondale & Redner 1990, 1994; Koponen 1994).

Trochosa terricola was evenly distributed along the sampling transects. Although Dondale & Redner (1990) suggest this species inhabits shady fields and forest edges, they reported a large number of *T. terricola* in a bog in southern Ontario (Dondale & Redner 1994). Since *T. terricola* was fairly abundant 2 m from shore, and also 20 m from shore, it does not seem to require particular micro-environmental conditions associated with the water's edge.

Distributions observed for the common linyphiids suggest that these spiders were common in a variety of habitats, and that none were strongly associated with the littoral zone community. Ground-dwelling linyphiids typically occupy the leaf-litter matrix in forests (Huhta 1971), and a variety of sources suggest that many species prefer closed-canopy forests (e.g., Pajunen et al. 1995; Buddle et al. 2000). Thus, sampling around a pond located in a closed-canopy forest is predicted to harbor higher catches of linyphiids than were found in our research. Since male and female *E. atra* were collected most frequently near the shore, this species was different from other linyphiids in that it seemed to remain near the pond shore. Although *E. atra* was considered rare in our collection (15 individuals), it is known to build webs adjacent to water, as reported by Kaston (1981); thus, more intensive sampling may show that this species has some moisture requirement and as such is closely tied to bodies of water.

Catches in the floating traps were distinct from other trap types along Axis 1 in our DCA. Traps >2 m from shore captured spider assemblages that blended into those from shoreline traps as evidenced by the species scores for *T. terricola*, *Grammonota gigas*, and *Pardosa moesta* in the DCA ordination (Fig. 5). In relative terms, these species may be considered generalists with respect to the types of terrestrial habitats tested in this study, and thus are common among terrestrial traps but rare in floating traps. Axis 1 of the DCA ordination explained much of the variation among trap captures, and supports the existence of a simple gradient of spider assemblages based on proximity to the pond: there are distinct spider assemblages (although not without overlap) associated with 1) the water's surface, 2) the habitat directly adjacent to the pond, and 3) the drier grass-dominated meadow located >2 m from the shore.

Without more intensive sampling, it is difficult to assess the habitat affinities of rarely collected species. However, we are able to comment on spiders collected in floating traps, as these had to arrive there via ballooning and/or skating across the water's surface. As such, a total of eight spider taxa have the potential to forage on the water's surface (Table 1), and collectively these spiders may be important predators in semi-aquatic food webs, as has been previously shown with *D. triton* (Zimmermann & Spence 1989.)

Soil moisture.—Few studies have directly examined how a moisture gradient might affect the relative abundance of spider species. Numbers of *Pirata piraticus* increased as soil moisture increased (Fig. 4C), corroborating the idea that this species requires high levels of moisture, higher humidity and lower ground temperature than other wolf spiders (Nørgaard 1951). Palmgren (1972) also suggested that this species is present along shores of freshwater bodies because it has a high light requirement. Therefore, *Pirata piraticus* is most likely adapted to littoral conditions where soil and vegetation are moist and temperatures are cool.

We know of no experiments investigating temperature and moisture requirements of *Pardosa fuscula*. Dondale & Redner (1990, 1994) suggest that this species prefers moist habitats including *Sphagnum* bogs, fens, marshes and meadows. *Pardosa fuscula* was more commonly found near the shore of a freshwater pond than in adjacent terrestrial habitats. Since males and females of this species showed this habitat affinity, it is likely that reproduction occurs close to the water's edge.

Pardosa moesta can be found in meadows, bogs and marshes (Dondale & Redner 1990), and in closed-canopy deciduous forests (Buddle 2000; Buddle et al. 2000). Dondale & Redner (1994) reported much higher numbers of *P. moesta* than either *P. fuscula* or *Pirata piraticus* in wet *Sphagnum* bogs. Although this was also true in our study, 65% of *P. moesta* were captured in the grass habitats >6 m from the pond shore. In addition, captures of this species were negatively associated with soil moisture (Fig. 4A). These results suggest that capture of *P. moesta* in terrestrial habitats is not driven solely by moisture conditions.

Trochosa terricola and the three common linyphiid species were active across much of the habitat gradient but were not significantly associated with our measures of soil moissture. Thus, these species do not have a strong association with soil moisture around our study pond. Opell & Beatty (1976) suggest that *Neoantistea* species build webs on the ground near water to condense moisture and thereby remain active during hot and dry times of the day. Although *N. magna* was common near the water's edge, it is probably not responding directly to moisture and instead may prefer areas where there are suitable depressions on which to anchor small sheet webs.

Semi-aquatic spiders.—We propose a new definition of a semi-aquatic spider as follows: a semi-aquatic spider species is one whose relative abundance is greatest on the water surface or close to the shore (i.e., within 2 m), and which may also have a significant preference or requirement for a moist substrate. Additionally, there must be evidence that these species reproduce on or near the water as inferred by collections of both male and female specimens at these locations. According to these criteria, three spider species from this study may be considered semi-aquatic. *Pirata piraticus* and *Pardosa fuscula* are both active at the pond shore and were strongly associated with moist substrates. *Dolomedes tri-*

ton was collected most often in the water where it walks easily across the surface and fishes for insect prey (Zimmermann & Spence 1989). Although other species in our study were collected more often near the shoreline (e.g., *N. magna*), their occurrence may reflect something other than strict requrirements for moisture. We also believe that more extensive sampling will reveal that some of the more rare species (e.g., *E. atra*) may also fit under our definition for semi-aquatic spiders.

Despite having been the subject of few ecological studies, there are diverse assemblages of spiders living along the gradient between a freshwater pond and its adjacent terrestrial habitats. Our study calls attention to this assemblage and shows that it is an interesting subject for ecological work. Some of these spiders clearly belong to a semi-aquatic or littoral spider community strongly associated with water. Additional studies of these species assemblages, their response to physical factors such as moisture, and role as predators in shoreline communities will provide greater understanding of the importance of semi-aquatic spiders in freshwater ecosystems.

ACKNOWLEDGMENTS

Funding for this work was provided by the Natural Science and Engineering Research Council of Canada (NSERC) in the form of an operating grant to JRS and a post-graduate scholarship to CMB. Many thanks to Donald J. Buckle for identifying the problematic linyphiids, and to the other members of the Spence laboratory for their patience and support.

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Manuscript received 10 May 2001, revised 6 March 2002.